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THE VELIGER

Observations on the Larval and Post-Metamorphic Life of *Concholepas concholepas* (Bruguière, 1789) in Laboratory Culture

by

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Abstract. Observations were made in the laboratory on the postcapsular life of the Chilean "loco," *Concholepas concholepas*. Spontaneously eclosed veligers were cultured on two separate occasions, initiated in October 1984 and in July 1985. Veligers fed on monospecific cultures of microalgae grew from an initial shell length of 250 μm to near 1700 μm during periods of 111 to 124 days. Of several tens of thousands of early larvae, only seven individuals could be brought through metamorphosis, of which only one survived and was cultured to juvenile size. About 60 competent veligers were captured at sea with a neuston net, and returned to the laboratory where about 50% passed metamorphosis. Of these, 11 were cultured to 10–20 mm during a 3-mo period.

Aspects of the external morphology, growth, and behavior of larvae and postlarvae are reported for the first time for this species. The larvae produce a four-lobed velum and employ a byssal thread for flotation. They produce a distinctive lip on the larval shell indicating readiness for metamorphosis. The propodium functions actively in adherence to substrates at metamorphosis, making this species highly adapted for recruitment in the wave-swept Chilean intertidal zone.

INTRODUCTION

Concholepas concholepas (Bruguière, 1789), an unusual muricid gastropod of the South American temperate west coast, is both biologically interesting and of high commercial value. It is the last surviving species of a genus whose other six members became extinct before or during the Pleistocene (STUARDO, 1979). The existing species, commonly referred to in Chile as the "loco," occurs from the intertidal zone to depths of 40 m, and has a geographical range from the central coast of Peru to the southern tip of Chile. Ecologically, locos are first-level carnivores that prey upon filter feeders such as the barnacles, mussels, and tunicates abundant on the rocky Chilean coast (CASTILLA *et al.*, 1979). Locos reproduce by depositing egg capsules on subtidal rocks, primarily during the winter months. After an incubatory period of one or two months, veliger larvae hatch from the capsules and enter the coastal plankton for periods estimated to be about three months, after which the later veligers settle in the high intertidal zone during the spring and summer months (CASTILLA, 1982).

Concholepas concholepas represents the largest gastropod fishery in the world (FAO, 1981). Fueled by a strong export demand beginning in the 1970s, landings of this species reached 24,858 metric tons (MT) by 1980 (CASTILLA & JEREZ, 1986). By 1984 the total catch had dropped to 11,100 MT (SERNAP, 1985) with declines in catch per unit effort demonstrated on a localized basis (GEAGHAN & CASTILLA, 1986). The author participated on an advisory panel in 1986 and 1987 convened by the Chilean national fisheries service (SERNAP) in order to help plan regulations designed to avoid overexploitation of the loco fishery. Among the panel's recommendations has been the need to study the planktonic and early recruitment phase of the loco life cycle, and the feasibility of its mass production under artificial conditions. Although numerous studies have been made on diverse aspects of the biology of the loco (see review in CASTILLA, 1982) it had not, until the present study, been cultivated in the laboratory.

The present study investigated aspects of the larval and postlarval biology of *Concholepas concholepas,* and used some elements of our bivalve hatchery facilities to examine the feasibility of its mass culture. The first successful laboratory culture of the species is now reported, with observations on its external morphology and behavior through the planktotrophic phase and metamorphosis. The behavior of loco veligers in laboratory aquaria led us to sample

for wild specimens in coastal surface waters. Success in this endeavor included the first recovery of advanced veliger larvae, followed by their metamorphosis and growth in the laboratory; these results lent critical support to the otherwise limited success of larval culture in the laboratory.

MATERIALS AND METHODS

Attempts at culture of postcapsular veligers of *Concholepas concholepas* were initiated in months when mature egg capsules became available in the local habitat. The first culture was initiated in October 1984 and the second in July 1985. Capsules were collected by a diver at 3–5 m, from the surfaces of subtidal rocks near the mouth of Herradura Bay (30°S); capsules containing mature larvae were chocolate brown in color. Capsules were maintained in unfiltered, aerated seawater, which was changed daily, at ambient temperatures near 16°C until hatching was observed. As these cultures involved trial and error in handling the larvae, we describe only the methods from the second culture which was more successful.

About 10^5 actively swimming veligers were collected on a 100-μm aperture nylon screen (Nytex Co.) within 16 h of their emergence from the capsules. The larvae were washed with 1-μm filtered, UV treated seawater, and distributed evenly by visual estimate into 10 10-L plastic pails. The water was renewed every other day. To avoid breakage of the fragile larval shells, the larvae were always caught on the 100-μm screen without removing it from the water (D'Asaro, 1965). Culture water was treated with 25 mg/L chloramphenicol (Merck Co.) during the first 10 water changes in an attempt to eliminate bacterial infections that might have been acquired within the capsule. After the early water changes, antibiotic treatment was administered as needed when microscopic examination showed incipient bacterial infections of the larvae.

A number of empirical trials were made with early larvae to determine acceptable temperature, food, and larval density; larval survival, growth, and behavior were used to evaluate the success of these trials. Larvae were offered monospecific cultures of microalgae that were available from our bivalve hatchery production system. These included *Tetraselmis* sp., *Pavlova* sp., *Chaetoceros* sp., *Isochrysis galbana* (Tahitian strain), and a *Pseudoisochrysis* sp. Advanced larvae were given small amounts of mixed algae of the above species in an attempt to vary the nutritive sources in addition to the daily monospecific food ration found to be best for early larvae.

Shell fouling of the larvae by bacteria and stalked protozoa sometimes mechanically interfered with larval swimming and contributed to a deterioration in water quality. Also, free-living protozoa and copepods occasionally appeared as contaminants in the cultures. These problems were treated by administering 1-min tap-water rinses to the larvae at the time of water change, usually eliminating the contaminants without observable effects on the larvae.

Larvae were routinely observed in a 25-mL plankton chamber using an inverted microscope, and were measured with a calibrated ocular micrometer. Shell length in this report refers to the major length from the tip of the siphonal canal to the apex of the shell as seen in silhouette. After metamorphosis, shell length was measured using the ocular micrometer in a stereo microscope, and later with a ruler, estimating to the nearest 0.5 mm. Calipers were not used owing to the risk of breaking the fragile shells. Some observations of shells and radulae were made using a JEOL Corp. model JSM T300 scanning electron microscope (SEM).

The single laboratory cultured postlarva that survived past metamorphosis in November 1985 was maintained in an aerated culture pail with daily changes of ambient seawater at room temperature of about 16–18°C. Initially the specimen was kept on a scallop shell that was collected from the local intertidal zone and was lightly fouled with microbial slime films, small polychaetes, barnacles, and bryozoans. At about 8 mm in length, it was transferred to a similarly encrusted stone collected from the low intertidal zone in the bay, upon which had been found a naturally recruited loco of about the same size. At about 12 mm in length, juveniles of *Semimytilus algosus* (Gould) were added to the system as prey.

Recovery of naturally occurring larvae from plankton was accomplished by towing a buoyed-frame neuston net, 2 m in length, with 600-μm mesh openings. The mouth of the net was rectangular, measuring 40 cm high by 80 cm wide, and was floated to sample the top 20 cm of the sea surface. One-kilometer hauls were made between December 1986 and March 1987, in and around the mouth of Herradura Bay. Loco veligers were recognized by their similarity to laboratory reared larvae, and were easily separated from other plankton by their tendency to fall to the bottoms of the collecting vessels and adhere firmly in place. Larvae were handled with a small camel's hair brush to avoid breaking their shells. Veligers so collected were introduced into a laboratory aquarium containing naturally encrusted stones from the intertidal zone and a constant flow of ambient seawater. The effluent pipe was screened with 1-mm mesh so as not to lose swimming veligers. These larvae were observed daily for evidence of metamorphosis and those passing metamorphosis were transferred to a rearing system where they were observed and measured periodically. Natural substrates used in setting and rearing were lightly populated by microbial slime films, crustose red, green, and brown algae, as well as by small barnacles, bryozoans, polychaetes, and sponges. Large invertebrates were eliminated, leaving some clean surfaces on the stones. Juveniles of *Semimytilus algosus* were added to the system as prey.

RESULTS

Of the many thousands of larvae placed in culture during two successive years, few larvae survived the experimental period to pass metamorphosis. Two larvae from the 1984

culture and five larvae from the 1985 culture passed metamorphosis; all other larvae died during the course of the cultures. Figure 1 plots the sizes of the largest larvae produced in the cultures over time periods lasting from 111 to 124 days. Of the five postlarvae produced in the 1985 culture, only one survived more than a few days and was raised to a size in excess of 20 mm (Figure 6).

Sources of Mortality

The veligers suffered chronic mortality punctuated by irregular mass mortalities at all stages of their development. Microbial diseases often appeared in the cultures, with at least four types of infection clearly definable. The first of these was internal necrosis of early larvae by a purple-pigmented microorganism that we believe, based on unpublished data, to be a bacterium contracted during the capsular developmental phase. A second type of infection was produced by a finely filamentous microorganism, extensively investing the mantle edge of the larvae, causing debilitation and death. Larvae infected in this manner failed to respond to antibiotic treatment, suggesting that the infection was fungal. A third type of infection included a green-pigmented microorganism that infected the basal region of the compound velar cilia, causing piecemeal loss of ciliary tufts. This infection could be arrested by the addition of chloramphenicol to the culture water; most larvae infected in this manner recuperated and regenerated the lost cilia. A fourth problem was attack of the larvae by a ciliate protozoan (*Tetrahymena* sp.), an occasional parasite that is capable of invading the larval digestive gland causing death of the host. This disease may be the primary cause of chronic mortality in cultures of *Concholepas concholepas* at all stages, and has also been the cause of mass mortalities of scallop postlarvae in our hatchery (unpublished data). No effective control measures have been found for this disease in the loco cultures. Other losses of larvae may be due to shell breakage during handling, although larvae do have limited capacity to repair damage to the leading shell edge and siphonal canal.

The following is a sequential account of events observed in our cultures, based on observation of the largest larvae recoverable at each time.

Early Larvae

Eclosion from capsules occurred slowly over several days. Most larvae swim actively in the water column, rising to the surface in ambient light directed from above. Some larvae, perhaps those not fully developed, settle to the bottoms of the eclosion pails. At this stage the protoconch measures 240–260 μm, and is semitransparent with tuberculate ornamentation (Figure 2A). The velum consists of two round lobes, each about 150 μm in diameter (Figure 2B). The head region between the velar lobes has eyespots on either side of the mouth (Figure 2C) and one short cephalic tentacle that is anteroventral to the right eyespot and has four apical sensory bristles. A pair of statocysts is visible posterior to the eyespots. At hatching the foot does not extend beyond the posterior border of the protoconch, is immobile, and has a few short sensory bristles at its posterior extremity. At hatching the larval gut retains a small amount of vitelline material which is utilized in a few days. Larvae begin feeding in 24–48 h, as evidenced by the appearance of microalgal food in the digestive tract. If food is withheld after the larvae begin feeding, die-off begins after 3 days with complete mortality after 7 days. Larval kidneys emerge from the mantle cavity and are lost at about 24 h after hatching. Shell growth begins soon after the initiation of feeding, appearing as successive increments on the protoconch.

Among the five species of microalgae offered to replicate samples of larvae in several trials throughout the culture period, *Isochrysis galbana* (Tahitian strain) was the most acceptable, as evidenced by digestion of the algal cells and the survival and growth of the larvae. Excessive numbers of microalgae in the water induce the veligers to produce mucus, which comes away from the larvae in thin, algal-laden strands. This material settles, producing undesirable organic contamination in the culture vessels. Acceptable initial culture conditions include one larva and about 2×10^5 microalgal cells per mL of culture water. As the larvae grow, the food ration is increased according to the larval capacity to ingest the algae without producing mucus strands.

The veligers appear to be positively phototactic throughout the entire culture period. When placed in cylindrical plankton chambers for observation with an inverted microscope they swim upward toward the light source and drop quickly to the bottom when the light is extinguished.

One to Three Weeks

By the end of the first week, a dorsocentral beak begins to form on the shell over the cephalic region and the siphonal canal develops on the left side of the shell. After about 10 days the shell begins to darken, and by three weeks it is dark amber-brown in color. Shell color is due to a periostracum that can be dissolved away with 0.1 N NaOH. At 10 days, black chromatophores are scattered over the dorsal surface of the foot, and the foot begins to show its first weak contractions. A few sensory bristles appear around the margin of the foot.

At about three weeks, a mantle tentacle appears inside the right mantle cavity, barely visible inside the shell edge. The velum has doubled its original size, and begins to show lateral indentations. The outer margin of the velum develops brown pigmentation demarcating the line of origin of the locomotory (compound) cilia.

Four to Seven Weeks

By four weeks the largest larvae have completed the first shell revolution around the protoconch, and measure about

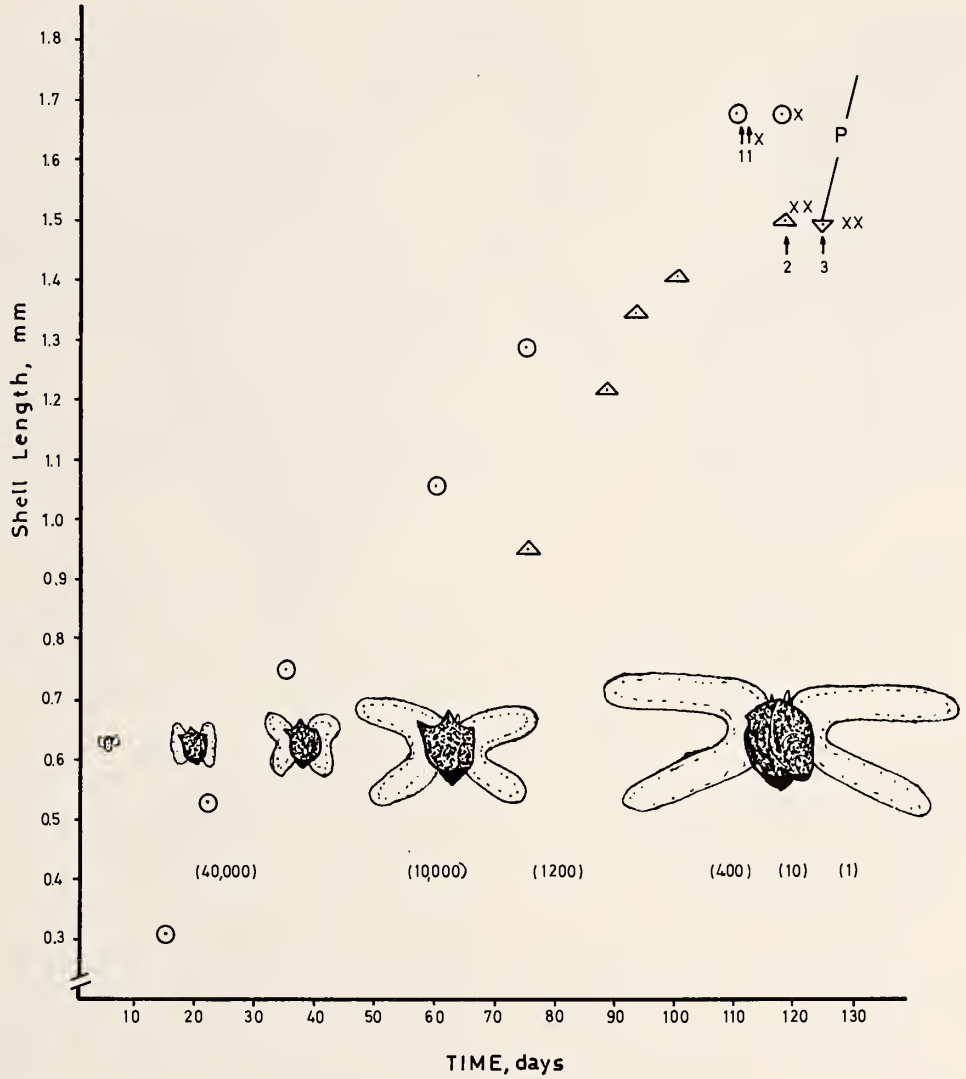


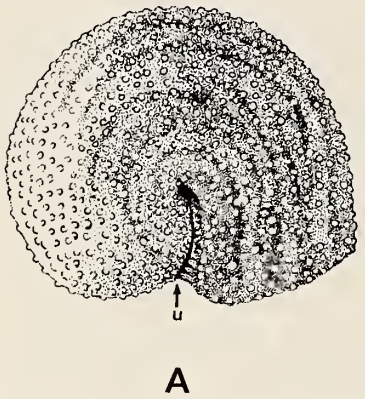
Figure 1

Sizes of largest individual veligers of *Concholepas concholepas* occurring in cultures initiated in October 1984 (circles) and July 1985 (triangles). Dorsal silhouette views of larvae show relative sizes of the larvae with time and development of the velum. Numbers in parentheses indicate approximate number of larvae surviving with time during the 1985 culture. Key: arrows, day of metamorphosis and number of specimens passing metamorphosis; X, death of a metamorphosed specimen; P, postlarval growth of single survivor, also plotted in Figure 6.

650 μm. The beak, with its central beak line, and the siphonal canal become prominent shell features (Figure 3). The shell becomes ornamented with radial lines (now coalescing from what began as lines of tubercles). The radial lines may act as reinforcement for the otherwise fragile shell. The velum has begun to elongate into four lobes, giving the veliger a "butterfly" appearance (Figure 3B). The velum remains unpigmented except for the outer margin. The single cephalic tentacle has begun to elongate and develop numerous sensory bristles.

The veligers swim freely in the culture pails at this stage, with no definable behavior pattern evident. The massing of larvae on the bottoms of the pails is often, although not always, a sign of developing disease or nutritional problems for a given group of larvae.

A notable development in the life of this veliger occurs beginning at 3–4 weeks with the appearance of a byssal thread issuing ventrally from a small gland at the extreme tip of the foot (Figure 3B). The byssal thread is about 1 μm in thickness and may extend for several centimetres. Larvae become capable of using the byssal thread for flotation, and are sometimes observed suspended in undis-



Figures 2A, B

External aspects of newly eclosed veliger larvae of *Concholepas concholepas,* shell length 260 μm. A. Right lateral view (shell only): u, umbilicus at center. B. Dorsal view: rt, right cephalic tentacle; lc, locomotory cilia.

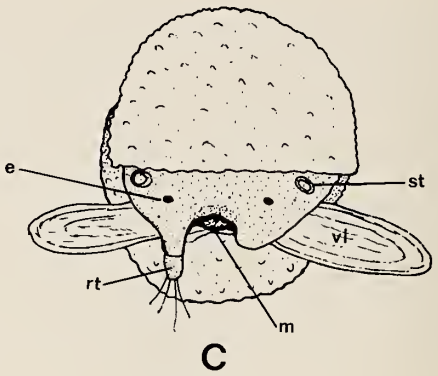


Figure 2C

Anterior view (locomotory cilia excluded): e, eyespot; st, statocyst; rt, right cephalic tentacle; vl, velar lobe; m, larval mouth.

turbed culture water with the thread adhering to the water surface film. These larvae could be gathered by inserting a dissecting needle through the air-water interface and catching the threads; threads were strong enough that individuals could be lifted from the water. Thread production could be induced in freely swimming larvae by short vigorous agitation of the culture water.

At about 40 days, the primordium of the second cephalic tentacle appears on the left side of the head region. The shell measures about 800 μm and has a pronounced beak. The four velar lobes become horizontally elongate and can measure a total width of 1350 μm when extended. The chromatophores on the foot become more numerous and diffuse, producing dark gray coloration; the foot increases its contractile movements. The propodial mucus gland appears as a horizontal slit across the anterior of the propodium, a structure that is now beginning to elongate and show independent movement. The secretion of a purple dye, typical of adult locos, is first observed at about 50 days as pigment granules deposited on the dorsum of the larval operculum.

Replicate cultures run between day 20 and 50 under the same conditions except for larval densities, showed significantly ($P = 0.95$) better growth of the larvae when maintained at densities of 250/L when compared with those at densities of 500 or 1000 larvae/L. Maximum shell length attained in these tests was 770 μm with 250 larvae/L, 624 μm with 500 larvae/L, and 562 μm with 1000 larvae/L. Individuals from a replicate culture with 250 larvae/L kept at 13–14°C were significantly ($P = 0.95$) smaller than those of the other groups maintained at 16–18°C; the maximum size recorded for this group was 580 μm. Unlike the other cultures, the cooler replicate experienced almost complete mortality near the end of the test period. Overall, larval densities had to be markedly decreased as the larvae grew in size, as they increasingly showed a tendency to become entangled with byssal threads or mucus strands. Nearing metamorphosis, the larval density had to be kept to 5–10 larvae/L.

Eight Weeks

The shell length measures 950–1000 μm, with about 20 μm added daily to the leading shell edge. The beak and siphonal canal continue to be prominent features of the shell. Larvae are capable of crawling on the foot for periods of up to 1 min during observations with the inverted microscope.

At 65 days, the extended foot measures about 950 μm, of which the propodium occupies about 200 μm. The propodium is about 200 μm in breadth when extended, and becomes active in dislodging mucus and algal debris from the velum and shell margin.

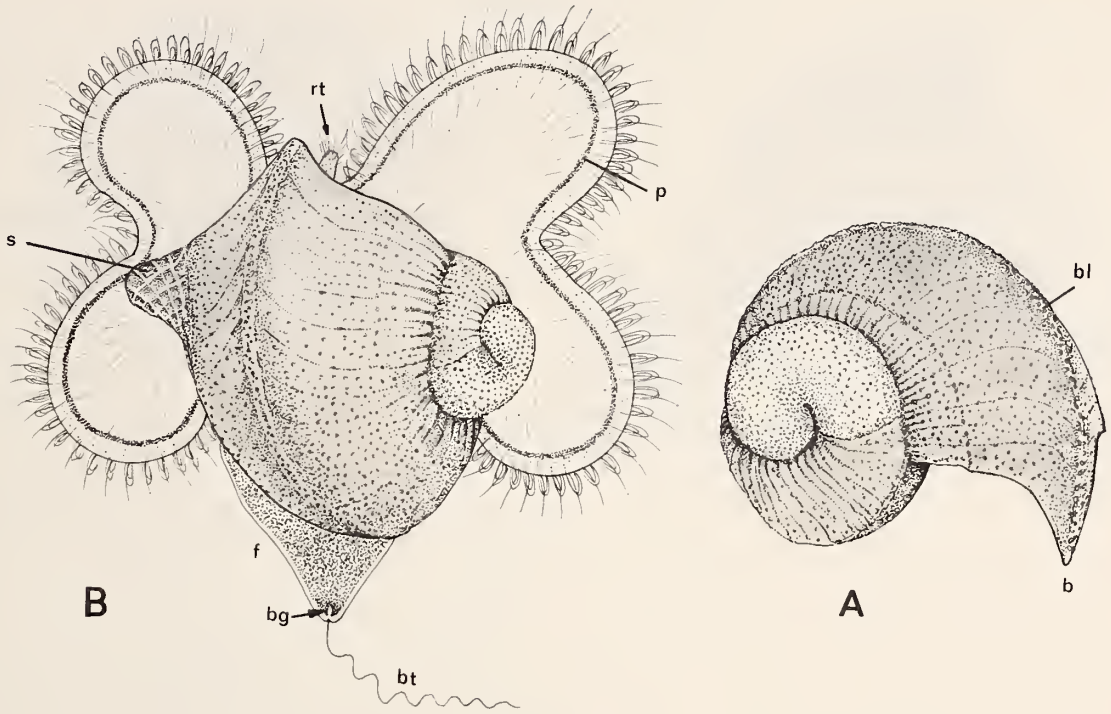


Figure 3

External aspects of one-month-old veliger larvae of *Concholepas concholepas,* shell length 650 μm. A. Right lateral view (shell only): b, beak; bl, beak line (crest). B. Dorsal view: bg, byssal gland; bt, byssal thread; f, foot; s, siphonal canal; rt, right cephalic tentacle; p, pigment.

Ten Weeks

Advanced larvae measure 1000–1200 μm in shell length, with a total velar extension of about 3200 μm. The right cephalic tentacle now measures about 260 μm in length, the left tentacle is about two-thirds this length, and the eyes are now located in the tentacle bases. The head and foot are now black, but the mantle edge, tentacle tips, and velum show little or no pigmentation. Veligers are capable of crawling on the foot for 3 min before they fall over. The operculum saddles the foot, is about 400 μm wide, and is stained purple.

At this stage larvae rarely swim, and are typically seen hanging by their byssal threads equidistant from one another in the culture water. The velum remains open and actively filtering. If released from the byssal threads, larvae drop to the bottom of the pail, but soon rise again in the water column. If they encounter the walls of the pail, they "push off" with a clapping motion of the velar lobes.

Twelve Weeks

The left tentacle reaches about three-quarters the length of the right tentacle. Shell growth has slowed, with largest veligers measuring 1400 μm (Figure 4). The gaps on either side of the beak have filled with shell, and the remnant of the beak is only a small projection.

Fourteen Weeks

Between 90 and 110 days, shell growth stops after completing 2.5 revolutions around the protoconch. Although early observations had suggested that ornamentation lines reflected daily growth increments, these "daily growth lines" could not be correlated with the known number of days in culture of the larvae. Using the SEM, what appeared to be true daily growth increments were demarcated by fine sutures in the shell. The cephalic tentacles are approximately equal in length, although the left tentacle tends to remain shorter than the right. The eyes project dorsolaterally near the base of each tentacle. A conical mentum, indicative of the site of the future opening of the postlarval mouth, is evident between the tentacles (Figure 4B).

The major event at this stage, indicating the termination of larval shell growth, was the production of an upturned lip around the leading edge of the shell (Figure 5). On two successive days metamorphosis was observed 24 h after the formation of the lip in each of two larvae from the culture initiated in October 1984 (Figure 1). Other lipped larvae from culture, as well as comparable larvae captured at sea, failed to undergo metamorphosis for days or weeks without further growth of the shell when maintained in clean culture vessels with microalgal food.

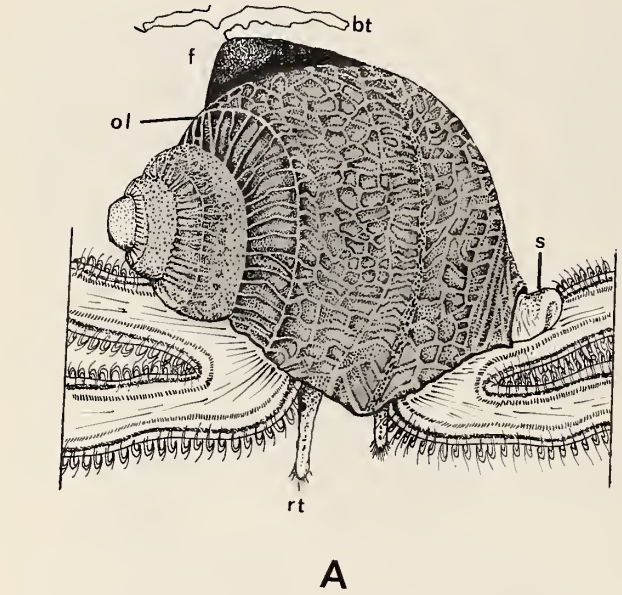
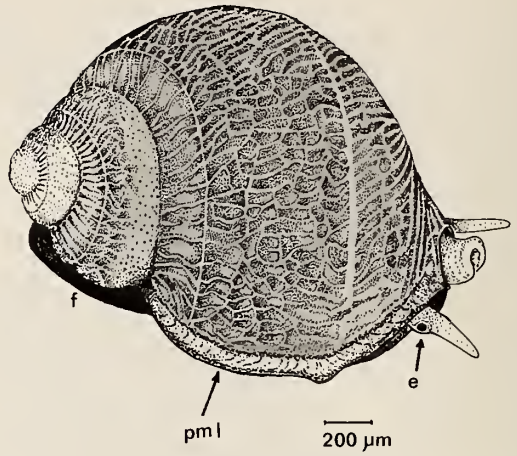


Figure 4

External aspects of three-month-old veliger larvae of *Concholepas concholepas*, shell length 1400 µm. A. Anterodorsal view: rt, right cephalic tentacle; s, siphon; ol, ornamentation lines; f, foot; bt, byssal thread. B. Anterior view of cephalic region (locomotory cilia omitted): SH, shell; s, siphon; me, mantle edge; e, eye; vl, velar lobe; rt, right cephalic tentacle; mt, mentum; m, larval mouth; po, post oral ciliary band; fg, food groove; pmg, propodial mucus gland; p, propodium; op, operculum.

The lipped shells of seven larvae from culture that passed metamorphosis measured between 1350 and 1690 µm in shell length, with velar extensions of up to 6500 µm. Thirty-one lipped larvae captured at sea measured between 1590 and 1830 µm ($\bar{x}$ = 1686; SD = 77).



Postlarval *Concholepas concholepas* prior to appearance of teleoconch, shell length 1690 µm: pml, premetamorphic lip; e, eye; f, foot.

Behavior Related to Settling and Metamorphosis

Development of a new behavior pattern becomes apparent after lip formation on the shell, preceding metamorphosis. The veliger acquires the capability of quick attachment to surfaces with which it comes in contact by the use of the suckerlike action of the (cupped) propodium. This behavior was first noted when attempting a routine transfer of lipped larvae with a glass pipette, to which they stuck immediately and with great tenacity.

At the lipped stage, veligers are capable of continuous crawling; we observed two of these veligers to settle on a natural substrate over which they crawled for periods of 24 h, after which they returned to a swimming existence. One veliger, accidentally left emersed for 8 h, returned to its swimming existence when returned to the water, and later passed metamorphosis. A further behavioral adaptation observed in lipped larvae may be referred to as "bubble capture." When strongly agitated by a jet of seawater from a hose, each veliger was observed to capture an air bubble using the foot, thus permitting it to float after loss of the byssal thread, and with the velum retracted. When left in calm water, each veliger released its bubble and resumed normal activity. This behavior was repeatedly elicited with dozens of larvae on different days.

Metamorphosis and Early Growth

Detailed observations of metamorphosis could not be made owing to the few larvae available and the unpredictability of the onset of metamorphosis. Of the total of seven larvae from the two laboratory cultures that passed metamorphosis, three died owing to accidents in handling, three failed to accept food and died without further growth in 3 to 7 days, and one survived and grew to juvenile size. The surviving postlarva was cryptic and difficult to find

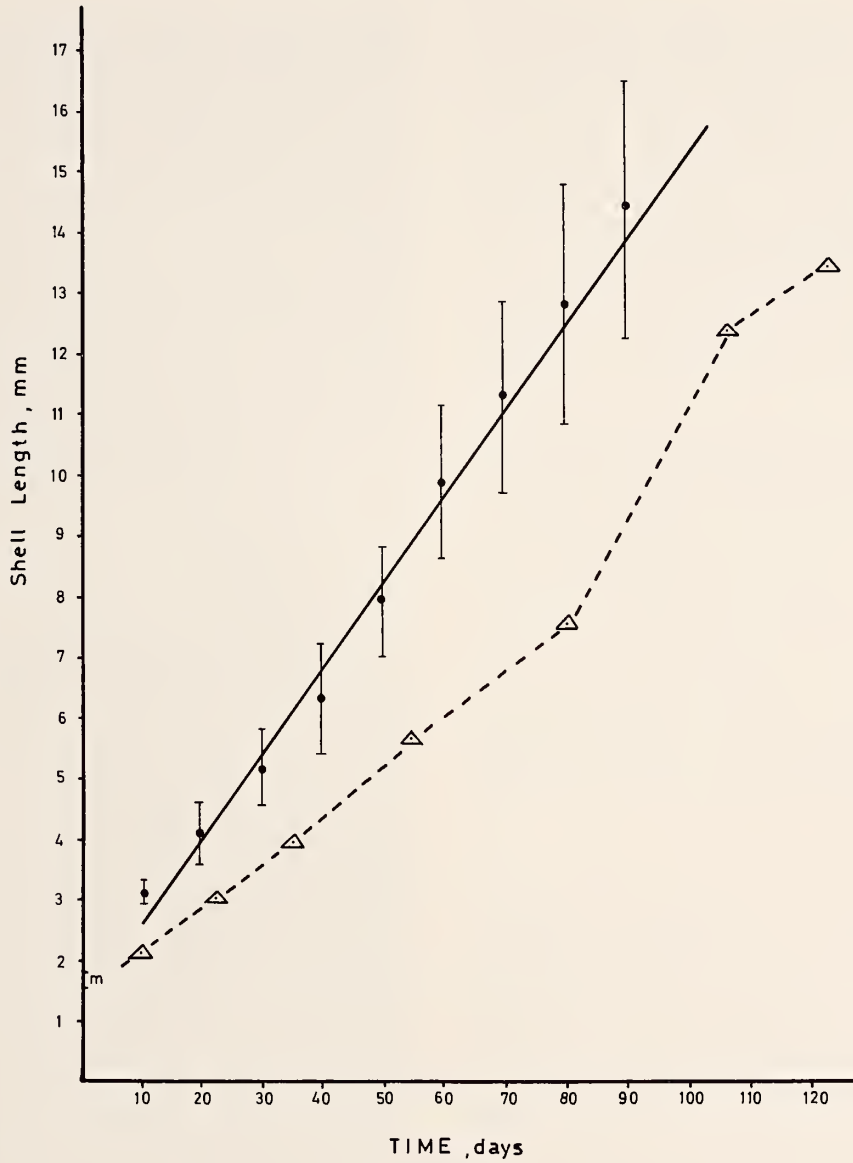


Figure 6

Growth after metamorphosis in the laboratory of 11 locos captured at sea as pre-metamorphic veligers (dots) ± 1 SD ($L_t = 1.16 + 0.143t$; $r = 0.98$). The growth of the single loco that survived through metamorphosis in laboratory culture is shown by the dotted line. m, sizes of specimens at metamorphosis.

while on its natural substrate. The first deposition of teleoconch material was observed at about 24 h post-metamorphosis as an extension of the siphonal canal. At about 48 h, the teleoconch became visible as a white ring around the shell margin. Teleoconch material deposited in the first few days was unpigmented, deposited in marked daily increments, and showed rugosity typical of advanced shells of *Concholepas concholepas*. A trunklike proboscis developed within 48 h of metamorphosis. This specimen grew to a size of 13.5 mm in the first four months post-metamorphosis (Figure 6). The first invertebrate prey taken by this specimen is unknown, although the specimen rasped the substrate at a very early stage, and later grazed on microalgae from the walls of the culture pail. Even after it began active predation on *Semimytilus algosus* it continued to graze clean 1–2 cm circular areas in a film of diatoms and bluegreen algae that had accumulated on the walls of the pail.

About 60 lipped larvae were captured at sea, half of which passed metamorphosis in the laboratory; 11 of these

survived the postlarval phase and were cultured to larger sizes (Figure 6). These veligers passed metamorphosis sporadically, rather than *en masse,* over periods of several days after their capture. Subsamples of this group failed to pass metamorphosis over a 48-h period when held in clean culture pails with aeration. Crawling veligers and postlarvae became negatively phototactic and were observed with difficulty on natural substrates owing to their small size, cryptic habits, and dark coloration. Remarkably, in a few days after metamorphosis, most of the black pigmentation disappeared from the head and foot, which assumed a whitish translucent color. Gray pigmentation was slowly regained by these structures, beginning about two months after metamorphosis.

Of all the crawling veligers observed, none was observed to possess a partially resorbed velum, suggesting that the loss of the velum is abrupt, possibly by swallowing (Fretter, 1967). Newly metamorphosed postlarvae are found on the cleanest available parts of the substrate, including unpopulated surfaces, barnacle shells, and calcareous algae. They possess a well-developed radula at metamorphosis, of which the rachidian teeth have a morphology distinct from those of adult *Concholepas concholepas* (Figure 7). Postlarvae rasp microbial films from both culture pails and natural substrates, leaving cleaned areas of several square millimetres daily. The digestive tract of a sacrificed 3-mm long postlarva reared on a natural substrate contained great numbers of bacteria, as well as some diatoms and a few fragments of fleshy encrusting red and brown algae.

The 11 specimens maintained in culture grew to 11–19 mm in length during the first 90 days, with a mean growth rate of 0.143 mm/day (Figure 6). They remained on a home range of about 10 × 20 cm on the underside of a stone during the day, and foraged over the whole stone at night. Upon reaching a few millimetres in size they began to perforate, paralyze, and consume animal prey.

DISCUSSION

The rearing of long-lived planktotrophic veliger larvae poses serious technical problems, as mentioned by D'Asaro (1965) in his study of *Strombus gigas.* Although there were similarities between the present study and that of D'Asaro, the rearing of *Concholepas concholepas* was even more problematical owing to the unusual longevity of these larvae. Personal communication with workers developing commercial cultures of *S. gigas* under proprietary conditions has suggested that the time to maturity of these larvae became progressively reduced as optimal feeding and handling methods were discovered. Similar advances may be expected in the culture of locos. The high levels of mortality in our cultures were disturbing, and reflect the present lack of knowledge concerning nutritional and environmental requirements of loco veligers. These larvae may indeed change food requirements as they grow and develop new organ systems (D'Asaro, 1965). Disease problems may be no more than a response to stress imposed by presently suboptimal culture conditions.

In the past, Castilla and co-workers (unpublished data) recovered molluscan larvae in vertical plankton hauls not far from our laboratory, but were unable to confirm the presence of advanced loco larvae in their samples owing to the unavailability of authentic reference specimens. Our experience with larvae in laboratory cultures allows the immediate recognition of loco larvae captured at sea. Our repeated collection of advanced veliger larvae in the surface plankton confirms observations made in the laboratory that these larvae tend to rise to the surface of the water column. On days when we captured naturally occurring loco larvae at the sea surface, hauls made with the same net towed at 2-m depth over the same transect captured none of these larvae. Metamorphosis and growth of field-captured larvae in the laboratory duplicated in a few days a result that had taken months to achieve by way of the time-consuming laboratory cultures.

Larval Strategies

The present laboratory and field observations suggest some of the evolved mechanisms whereby *Concholepas concholepas* has survived and become widely distributed, and permits hypothetical reconstruction of the natural history of the larval phase of the life cycle. Larvae may require up to four months to reach the lipped form, ready for metamorphosis. Lipped larvae may survive for many more weeks, suspended by the byssal thread and feeding while drifting in oceanic currents in a manner similar to that described by Sigurdsson *et al.* (1976) for plantigrade bivalve larvae. (Kensley [1985] discovered a relict fossil population of locos in southwest Africa which he attributed to the possible long distance dispersal of larvae by the West Wind Drift.) Larvae may maintain themselves near the water surface by velar swimming governed by their positive phototaxis. They may thus be maintained near the coastline by surface circulation driven by prevailing onshore winds active during the daytime. Byssal threads inserted in the air-sea interface may tow larvae along the surface when acted upon by these winds. Upon arrival at the shore, larvae tossed by the surf may effect "bubble capture," maintaining themselves in the neuston to be carried ashore with the surface slick or in sea foam. Upon being cast ashore, larvae quickly settle on the rocks using the propodium, seek a protected spatial niche, metamorphose, and begin feeding on microbial films. They become cryptic inhabitants of the rocky shore infauna until they have produced a resistant shell and can begin active feeding on invertebrates.

All 60 larvae caught by us at sea during a two-month period were competent for metamorphosis (lipped). These may have been the last individuals representing the reproductive cohort hatched during 1986, assuming that the majority of larvae of that year class had recruited to the plankton by August (Castilla, 1982). The early growth

of postlarval locos (Figure 6) appears to be linear during the first few months of life, and may be continuous with the growth curve obtained by GUISADO & CASTILLA (1983) for naturally occurring populations ranging in size from 11 to 57 mm. We do not know what factors induce metamorphosis in loco veligers, although chemosensory recognition of suitable substrates probably plays an important role (MORSE *et al.*, 1980).

Observation of algal feeding by juvenile locos is not inconsistent with known omnivorous feeding patterns observed in life histories of other juvenile muricids (M. R. Carriker, personal communication), but it is remarkable that algal feeding did not cease even after the young locos had begun to feed actively on mussels. Also remarkable is the finding that the radular teeth of the postlarva were distinct from those of the adult (Figure 7).

Prospects for Mass Culture

The limited knowledge presently available from our laboratory cultures of *Concholepas concholepas* suggests that mass commercial culture of this species is infeasible in the near future. Larval locos are simply not suitable for the presently used techniques of tank culture. Possession of a large, fragile, and efficient velum, as well as a highly specific mechanism for flotation (byssal thread), has adapted this species to a solitary drifting existence in oceanic waters. A widely separated distribution at the sea surface was demonstrated during our plankton hauls, where the net had to be towed several kilometres to obtain a very few larvae. On our most successful day in January 1986 we obtained a total of 47 larvae from seven separate 1-km hauls. Implications of this mode of life for hatchery design include maximization of culture volume per larva, continuous feeding with dilute suspensions of microalgae, and maintenance of high water quality for extended periods of culture. If such conditions are not maintained, larvae become entangled with byssal threads or mucus strands, fall to the tank bottom, and are subject to microbial attack.

The above-mentioned hatchery requirements are uneconomical compared with methodology used in mass rearing of bivalve larvae (DISALVO *et al.*, 1984) or lecithotrophic gastropod larvae (OWEN *et al.*, 1984), which can be maintained at high densities and pass metamorphosis in a few days or weeks. Mass culture of the loco might be based on the capture of lipped veligers at sea, with transfer to hatchery settling and rearing systems. Presently, such development is limited by the lack of knowledge of season and geographic location of larval concentrations off the coastline.

Resource Management

If culture seems a distant possibility, then preservation of the resource lies now in the correct management of remaining natural stocks. Such management has been hindered by logistical difficulties in the estimation of population parameters. The procedure of capturing pre-metamorphic larvae at sea provides a new method for the indirect monitoring of the reproductive success of the remaining stocks of locos. This technique can be made at least semi-quantitative by the establishment of standard transects to be monitored routinely throughout the year, and calculating the number of competent larvae per km^2 of sea surface. Yearly counts of competent larvae near shore could provide information on long-term trends in the reproductive success of the loco in the face of continued harvesting pressure. The method proposed is unsophisticated and inexpensive compared with diver surveys of loco populations and with shoreside censuses of fishery success, which are subject to many sources of bias. The measurement proposed would not, however, predict actual recruitment to the population, which should be measured by other means and then correlated with larval counts.

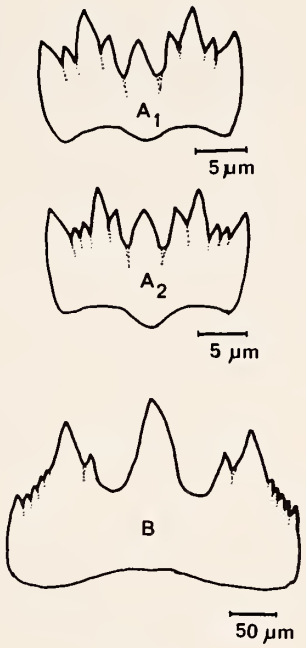


Figure 7

Rachidian teeth from a postlarval *Concholepas concholepas*. A_1 from anterior teeth; A_2 from posterior teeth. Adult loco rachidian tooth (B) presented for comparison of form.

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NOTE ADDED IN PROOF

On 21 September 1987, 24 lipped veligers ($\bar{x}$ = 1780 μm, SD = 100 μm) were captured in a surface plankton haul about 2 km seaward of the mouth of Herradura Bay. These larvae were returned to the laboratory setting system containing a natural substrate as described in the text, with a continuous flow of seawater of 10 L/min at 15°C. This flow rate rate caused agitation within the system, and circulation of the veligers over the substrate. Within 16 h (overnight) 22 of these veligers had passed metamorphosis, settling both on the substrate and walls of the aquarium. This was taken as evidence that these larvae could pass metamorphosis *en masse* in the presence of turbulent water.